

SOME NEW AND RECONSIDERED CALIFORNIA
DUDLEYA (CRASSULACEAE)

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ABSTRACT

Three new taxa of *Dudleya* from California are described: *Dudleya cymosa* subsp. *agourensis*, *D. cymosa* subsp. *crebrifolia*, and *D. abramsii* subsp. *affinis*. Three new combinations of *Dudleya* also are proposed from California: *D. cymosa* subsp. *pumila*, *D. cymosa* subsp. *paniculata*, and *D. abramsii* subsp. *callicola*. *Dudleya gigantea* is reduced to a synonym of *D. cymosa* subsp. *cymosa* and *D. minor* is reduced to a synonym of *D. lanceolata*. A neotype is designated for *Echeveria cymosa* Lem. (= *D. cymosa* subsp. *cymosa*).

Recent collections made during a study of the *Dudleya cymosa*–*abramsii* complex revealed some undescribed taxa and a need to re-evaluate others. *Dudleya* species often exhibit considerable phenotypic plasticity resulting from the variability of climatic conditions, soil, and exposure that often alters, sometimes quite dramatically, the appearance of the same plant from year to year. Although morphological measurements taken from the field are important to accurately identify many plants, field measurements from succulent plants like *Dudleya* often have proven to be unreliable. Therefore, the interpretation of each taxon discussed here will rely heavily on data obtained from cultivated plants in an effort to reduce variability in certain morphological characters (e.g., leaf size and shape, floral stem length, inflorescence shape, pedicel length, etc.) that are used in determining taxa. This approach makes it possible to evaluate under a uniform and stable environment those characters that apparently are controlled genetically.

MATERIALS AND METHODS

In collecting live material for study, five plants were selected by tossing a 10 cm hoop within an area greater than 9 m² where there were many flowering plants of *Dudleya*. The first five plants selected were measured in the field and then collected for cultivation studies.

Herbarium and living specimens were examined. Most of the floral measurements were obtained from wild or cultivated living material. Because of the tendency for certain flower parts, in particular the staminal filaments, of *Dudleya* to continue to grow even after the

flower appears to be fully mature, all measurements were taken two days following anther dehiscence.

Cultivated plants were grown at Hawthorne, California (33°55'N, 118°22'W), in a structure constructed with a clear fiberglass roof and 30% shade cloth for the sides. An artificial soil was used that consisted of two parts fine redwood shavings, two parts coarse Canadian peat moss, two parts diatomaceous earth, one part sand, and one part fine perlite. One kg of milorganite was incorporated for each m³ of medium. The medium was then moistened and aged for a minimum of one month.

Flower buds used for cytological observations were collected from cultivated plants between 0930 and 1000 hr and fixed in a modified Carnoy solution (Uhl and Moran 1953), which consisted of chloroform, EtOH, and glacial acetic acid (3:2:1, v/v/v). Counts were made from a minimum of five buds.

TAXONOMIC TREATMENT

- DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. CYMOSA—*Echeveria cymosa* Lemaire, Revue Hort. 7:439. 1858.—*Cotyledon cymosa* Baker in Saunders, Refug. Bot. 1:pl. 69. 1869.—*Dudleya cymosa* Britton & Rose, Bull. N.Y. Bot. Gard 3:21. 1903.—*Cotyledon laxa* var. *cymosa* Jepson, Man. Fl. Pl. Calif. 453. 1925.—*Echeveria laxa* var. *cymosa* Jepson, Fl. Calif. 2:114. 1936.—Neotype: Plate in Saunders, Refug. Bot., pl. 69. 1869.
- Dudleya gigantea* Rose in Britton & Rose, op. cit. p. 23.—*Cotyledon gigantea* Fedde, Bot. Jahresber. Just. 31:826. 1904.—*Echeveria amadorana* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:479. 1930 (based on *Dudleya gigantea* Rose).—TYPE: USA, CA, Amador Co., New York Falls, ca. 1500 ft (460 m), 15 Jun 1896, G. Hansen 2012 (Holotype: US! (US 338497), photo LA!; isotype: CAS!, NY!).
- Echeveria lanceolata* var. *incerta* Jepson, Fl. Calif., p. 115. 1936.—TYPE: USA, CA, Calaveras Co., Calaveritas Creek, near Kentucky House, ca. 900 ft (275 m), 27 May 1923, W. L. Jepson 9919 (Holotype: JEPS!, photo LA!).

Caudex short, usually less than 5 cm long, 1–3.5 cm diam., unbranched or few branched. Basal rosettes 6–20(–25) cm diam., consisting of 6–25 oblanceolate to rarely spatulate leaves, acute, acuminate or, infrequently, cuspidate, 2–17 cm long, 1.5–6 cm wide, and 1–5 mm diam. Floral stem 0.5–4.5 dm tall, 2–8 mm diam., with 7–20(–30) horizontal to ascending ovate to triangular-lanceolate leaves, acute to acuminate, the lowermost 0.5–3(–10) cm long and 5–15 mm wide. Inflorescence obpyramidal, infrequently paniculate or simple, commonly with 2–4 branches that rebranch 0–3 times; cincinnus circinate when young, ascending in age, 1–5(–15) cm long

and (1-)2-10(-20) flowers; pedicels erect, the lowermost 5-15 mm long, 0.5-2 mm diam. Calyx 3-7 mm long, 2.5-6 mm wide, rounded to truncate below; lobes triangular to triangular-ovate, acute to \pm acuminate, 1.5-5 mm long, 1.5-4 mm wide. Corolla ovoid in bud, cylindrical in anthesis, often with the petal apices spreading from 45°-90°; petals yellow, orange, or red, occasionally glaucous along the midrib, elliptic to narrowly lanceolate, acute, 7-15 mm long, 2-4 mm wide, connate 1-2.5 mm; filaments 4-8.5 mm long, adnate for 1-3.5 mm, the epipetalous mostly 0.5 mm shorter and adnate, mostly 0.5-0.7 mm higher than the antesealous; anthers yellow, 1-2 mm long. Gynoecium 4-10 mm long, erect when young, slightly spreading in age, ovaries 3-8 mm long, styles 1-2 mm long. Nectaries reniform, 1-2 mm wide. Chromosome number: $n = 17$. Flowering April to July.

Distribution. USA, California: Coast Ranges from Humboldt Co. to Santa Clara Co.; Sierra Nevada. Elev. 100-2700 m.

Based on the original description, the type locality is probably in California ("... corolles jaune-pâle. Californie? Très distincte!"—Lemaire 1858). According to Moran (1951), no authentic specimen is available; however, he noted that Lemaire's plant came from the horticulturist Louis de Smet of Ledeburg, Belgium, in or before 1858, and the plant illustrated by Baker in *Saunders Refugio Botanicum* came from a horticulturist in nearby Ghent in 1855 and probably was of the same introduction. Because the plate compares well with the original description and clearly illustrates most of the plants presently referred to *Dudleya cymosa*, this plate serves as the neotype until an authentic type specimen is found.

Based on its greater average size when compared with *D. cymosa* subsp. *cymosa*, Moran (1951, 1957) recognized *Dudleya gigantea* as a subspecies of *Dudleya cymosa*. Moran (1951) noted, however, that there was a dwarf specimen on the type sheet. He also mentioned that subsp. *cymosa* occurs at nearby localities, with no evident natural barriers. As a result of additional collections and the data from cultivation, the size difference between *D. gigantea* and *D. cymosa* is not apparent and, thus, there is not enough evidence to warrant maintaining *D. gigantea* as a distinct taxonomic entity.

Moran (1951, 1960) reduced *Echeveria lanceolata* var. *incerta* to a synonym of *Dudleya cymosa* subsp. *gigantea*. Variety *incerta* also does not appear to be different from *D. cymosa* subsp. *cymosa*.

Dudleya cymosa* subsp. *pumila (Rose) K. Nakai, comb. nov.—*Dudleya pumila* Rose, Bull. N.Y. Bot. Gard. 3:14. 1903.—*Cotyledon pumila* Fedde, Bot. Jahresber. Just. 31:826. 1904.—*Echeveria parva* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a: 477. 1930 (based on *Dudleya pumila* Rose).—TYPE: USA, CA,

San Bernardino Co., San Bernardino Mtns., between Green Valley and Deep Creek, 7000 ft (2120 m), 19 Jul 1899, *H. M. Hall 1350* (Holotype: US!, photo DS!, LA!; isotype: UC!).

Distribution. USA, California: South Coast Ranges from Monterey Co. south to the San Gabriel and San Bernardino mtns. Elev. 100–1800 m from Santa Barbara Co. north, 600–2600 m from Ventura Co. south.

Rose (1903) based *D. minor* on two collections [*Rose 421* (ex *Hasse*) (NY, US), 1893 *McClatchie* (NY, UC)]; both were collected from San Gabriel Canyon. Moran (1957) reduced *D. minor* to a subspecies of *D. cymosa*. Munz (1959, 1974) lists *D. cymosa* subsp. *minor* from the Santa Lucia Range in Monterey Co. south into the Transverse Range of southern California.

I was unable to find any dudleya resembling the many herbarium specimens labeled *D. minor* or *D. cymosa* subsp. *minor* (Rose) Moran at the type locality. Although the original description suggests a relationship with *D. cymosa* based on leaf shape, pedicel length, and petal shape, I have determined that the holotype of *D. minor* resembles plants intermediate between *D. cymosa* and *D. lanceolata* (Nutt.) Britt. & Rose.

In southern California, *D. cymosa* is usually a small plant, mostly 5–8 cm in diameter. In the central portion of the Transverse Ranges, the rosette leaves are mostly oblanceolate to spatulate. The floral stem is usually less than 15 cm tall, the inflorescence is rather compact with 4–8 flowers per cincinnus. The lowermost pedicels are often at least as long as the length of the corolla. *Dudleya cymosa* is a diploid ($n = 17$; Uhl and Moran 1953).

Dudleya lanceolata is often larger, 8–12 cm in diameter. The rosette leaves are typically oblong to lanceolate or infrequently elliptic to ovate. The floral stem is usually greater than 15 cm tall, the inflorescence is often lax with 6–15 flowers per cincinnus. The lowermost pedicels may be as long as the corolla, but usually they are much shorter. *Dudleya lanceolata* is a tetraploid ($n = 34$; Uhl and Moran 1953).

The shape of the basal rosette leaves and the length of the pedicels of the holotype of *D. minor* suggest a relationship with *D. cymosa*, whereas the length of the floral stem, the more lax inflorescence, and the greater number of flowers per cincinnus is similar to *D. lanceolata*. Indeed, most of the dudleyas observed from elevation 500–1000 m were clearly *D. lanceolata*; however, a few individuals resemble *D. cymosa* morphologically even though cytologically they were tetraploids.

For comparison of *Dudleya minor* with *D. cymosa* and *D. lanceolata*, dudleyas were collected along California State Highway 39, which travels through San Gabriel Canyon, at elevational increments

of 100 m from 500–1700 m. Morphological measurements were made in the field. The plants were then cultivated and the same measurements were repeated the following year and chromosome counts were made. The measurements were translated into numerical values or scores so that the sum of the total characters from each population may be compared (Table 1, Fig. 1). Voucher specimens were deposited at LA.

Figure 1 shows there is a distinct break in morphological measurements between 1200–1500 m. Wild plants from 500–1200 m had an average score of 11.5, whereas those from 1500–1700 m had an average of 18.7. Cultivated plants displayed a similar break, although less than that found in wild plants (13.3 vs. 19.0). The chromosome number also correlated with elevation. Tetraploid plants occurred below 1200 m and diploid plants occurred above 1500 m. Based on morphology and chromosome number, *D. lanceolata* apparently occurs from 500–1200 m and *D. cymosa* is found above 1500 m in San Gabriel Canyon.

Although the type specimen of *D. minor* may resemble *D. cymosa*, it was collected below 1200 m. Thus, on the basis of morphological and cytological data obtained from both wild and cultivated plants I consider *D. minor* to be conspecific with *D. lanceolata*. Because the type specimen of *D. pumila* Rose represents most of the *D. cymosa* in southern California, I propose the combination *D. cymosa* subsp. *pumila* to replace *D. cymosa* subsp. *minor*.

- Dudleya cymosa** subsp. **paniculata** (Jeps.) K. Nakai, comb. nov.—*Cotyledon caespitosa* var. *paniculata* Jeps., Fl. W. Mid. Calif. 267. 1901.—*Dudleya paniculata* Britt. & Rose, Bull. N.Y. Bot. Gard. 3:27. 1903.—*Cotyledon paniculata* Fedde, Bot. Jahresber. Gard. 31:826. 1904 (non *C. paniculata* Thunberg.).—*Echeveria jepsonii* Nelson & Macbride, Bot. Gaz. (Crawfordsville) 56:477. 1913 (based on *Cotyledon caespitosa* var. *paniculata* Jeps.).—*Cotyledon laxa* var. *paniculata* Jeps., Man. Fl. Pl. Calif. 543. 1925.—*Echeveria laxa* var. *paniculata* Jeps. Fl. Calif. 2:114. 1936.—TYPE: USA, CA, Alameda Co., Morrison Canyon, 20 Jun 1897, *W. L. Jepson 13419* (Holotype: JEPS!, photo LA!).
- Dudleya humilis* Rose, Bull. N.Y. Bot. Gard. 3:27. 1903.—*Cotyledon humilis* Fedde, Bot. Jahresber. Just. 31:826. 1904 (non *C. humilis* Marloth. 1915).—*Echeveria diaboli* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:480. 1930 (based on *Dudleya humilis* Rose.).—TYPE: USA, CA, Contra Costa Co., summit of Mt. Diablo, 2 Jun 1903, *Alice Eastwood s.n.* (Rose 620) (Holotype: US!, photo LA!; isotype: NY!).

Distribution. Inner South Coast Range from Contra Costa Co. south to western Fresno and northeastern Monterey cos.

Moran (1951, 1960) considered *Cotyledon caespitosa* var. *paniculata* a synonym of *Dudleya cymosa* subsp. *setchellii* (Jeps.) Moran. He noted, however, that they might be separated on the basis of the rosette leaf shape. Based on studying 34 herbarium specimens and 100 live plants from 20 populations of subsp. *paniculata* and 13 herbarium specimens and 20 live plants from four populations of subsp. *setchellii*, I found that subsp. *paniculata* differs from subsp. *setchellii* by having oblong to oblanceolate basal rosette leaves compared with oblong-triangular leaves, an inflorescence of 2–3 branches that rebranch one or twice rather than 2–3 mostly simple branches, and pedicels 6–12 mm long versus 4–7 mm long. Subspecies *setchellii* is restricted to the serpentine rock outcrops within the Santa Clara Valley, whereas subsp. *paniculata* occurs within the Inner South Coast Range on various rock substrates.

Dudleya humilis Rose is reduced to a synonym of *D. cymosa* subsp. *paniculata*. A similar form [K. Nakai 816 (LA)] was collected near the summit of Mt. Hamilton, which is south of Mt. Diablo, the type locality of *D. humilis*. *Dudleya humilis* appears to be an edaphic dwarf of subsp. *paniculata* because cultivated plants I have grown from each location did not appear different from cultivated plants of subsp. *paniculata*.

***Dudleya cymosa* subsp. *agourensis* K. Nakai, subsp. nov.**

A subspecies typica caulis ramosus, rosulae foliis 6–10, glaucis, ellipticis vel oblongis differt. Figs. 2a,b, 5.

Plants simple or with six or more caespitously branched rosettes 5–10 cm diam., with 6–10 elliptic to oblong glaucous leaves. Basal rosette leaves 3–10 cm long, 1–1.5 cm wide, acute to acuminate; cauline leaves lanceolate, glaucous, 1–2.5 cm long, 7–10 mm wide, acute to acuminate. Floral stem erect, 10–20 cm tall, glaucous, often tinged with red; inflorescence of 2–3 simple to bifurcate branches; cincinnus ascending, 1–3 cm long with 3–8 flowers; lowermost pedicels 6–12 mm long. Petals bright yellow, occasionally glaucous along the midrib, petal apex spreading 45–90°. Chromosome number: $n = 17$. Flowering May to June.

TYPE: USA, CA, Los Angeles Co., Santa Monica Mtns., ca. 0.5 km s. of the junction of Agoura and Cornell roads on Cornell Road, 34°08¼'N, 118°45½'W, on nw.-facing volcanic rock road embankment, locally abundant, 275 m. Associated with *Malosma laurina*, *Haplopappus linearis*, *Dichelostemma pulchella*, *Delphinium parryi*, *Calochortus venustus*. 27 May 1980, K. Nakai 606 (Holotype: CAS; isotype: LA, SD).

PARATYPES: Los Angeles Co., w. of Calabasas Moran 3472 (UC); Agoura, along Cornell Road, Nakai 436 (LA); n.-facing volcanic

TABLE 1. CONTINUED.

| Elevation (m) | Rosette dia- meter (cm) | | Rosette leaf shape | | Rosette leaf length (cm) | | Floral stem length (cm) | | Inflorescence | | Number of flowers per cincinnus | | Lowermost pedicel length (mm) | | Chro- mo- some num- ber (n) | Score |
|------------------|----------------------------|------|--|------|-----------------------------|------|----------------------------|-------------------|---------------|-----|---------------------------------------|------|-------------------------------------|------|--|-------|
| | \bar{x} | s.d. | | | \bar{x} | s.d. | \bar{x} | s.d. | | | \bar{x} | s.d. | \bar{x} | s.d. | | |
| 1000 | none found | | | | | | | | | | | | | | | |
| 1100 | | | | | | | | | | | | | | | | |
| W | 12.0 | 2.5 | oblong to oblanceolate | 10.3 | 2.0 | 19.3 | 6.2 | lax | 13.5 | 5.3 | 6.0 | 0.0 | 11 | | | |
| C | 6.0 | 0.5 | oblong to | 3.5 | 0.7 | 11.0 | 3.1 | lax | 8.0 | 2.5 | 6.0 | 0.0 | 34 | | | |
| 1200 | | | | | | | | | | | | | | | | |
| W | 13.0 | 3.6 | ovate to lanceolate | 11.5 | 3.8 | 13.4 | 2.5 | lax | 11.0 | 4.2 | 8.5 | 1.0 | 12 | | | |
| C | 10.0 | 1.1 | oblanceolate | 7.5 | 0.5 | 11.0 | 3.1 | lax to compact | 9.3 | 2.1 | 10.0 | 1.0 | 34 | | | |
| 1300 | none found | | | | | | | | | | | | | | | |
| 1400 | none found | | | | | | | | | | | | | | | |
| 1500 | | | | | | | | | | | | | | | | |
| W | 6.5 | 1.5 | rhombic- oblanceolate to spatulate | 4.3 | 0.8 | 6.5 | 1.0 | compact | 6.0 | 2.0 | 10.0 | 0.5 | 18 | | | |
| C | 5.5 | 1.5 | spatulate to rhombic | 4.0 | 0.8 | 4.0 | 0.8 | compact | 5.0 | 2.0 | 11.0 | 1.0 | 17 | | | |
| 1600 | | | | | | | | | | | | | | | | |
| W | 6.0 | 0.8 | spatulate | 5.3 | 0.5 | 7.0 | 1.7 | compact | 5.5 | 3.0 | 9.5 | 1.5 | 18 | | | |
| C | 6.0 | 0.8 | spatulate | 5.5 | 0.4 | 3.5 | 0.7 | compact | 6.0 | 1.0 | 10.0 | 1.0 | 17 | | | |
| 1700 | | | | | | | | | | | | | | | | |
| W | 4.5 | 0.9 | spatulate | 3.0 | 0.6 | 4.5 | 0.9 | compact | 6.0 | 2.5 | 11.0 | 1.0 | 20 | | | |
| C | 4.5 | 0.9 | spatulate | 3.0 | 0.6 | 3.0 | 0.3 | compact | 4.0 | 1.0 | 9.0 | 1.0 | 17 | | | |

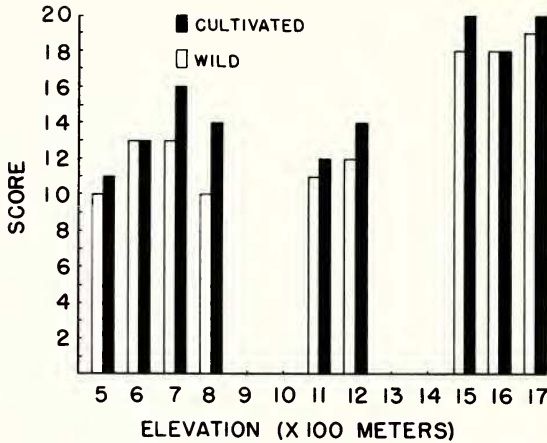


FIG. 1. Bar graph illustrating index score vs. elevation derived from Table 1 for *Dudleya cymosa* and *D. lanceolata* as collected from along California State Highway 39. □ = wild plants; ■ = cultivated plants.

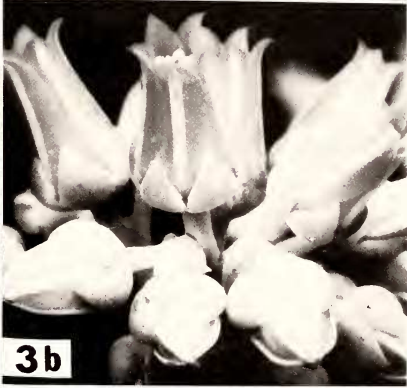
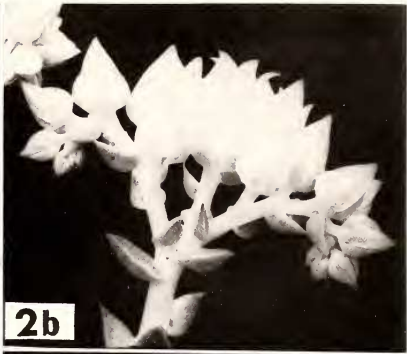
slopes of Ladyface Mountain, 400 m, *Nakai 1119* (CAS, LA); rocks on the e. side of State Hwy. 23 near the jct. of Portrero Road and Hwy. 23, 365 m, *Nakai 512* (LA). Ventura Co., n.-facing volcanic rock along Hwy. 23 e. of Lake Eleanor, 300 m, *Nakai 607* (CAS, LA).

Distribution. North slope of the western portions of the Santa Monica Mtns.

Dudleya cymosa subsp. *agourensis* differs from subsp. *cymosa* by having rosettes consisting of 6–10 elliptic to oblong leaves rather than 10–25 leaves that are oblanceolate to spatulate. Uhl and Moran (1953) placed a population of subsp. *agourensis* (*Moran 3472*) with *D. cymosa* subsp. *ovatifolia* (Britt.) Moran. Nakai (1983) considered this population a distinct race of subsp. *ovatifolia*. Subspecies *ovatifolia* also occurs in the Santa Monica Mountains and, like subsp. *agourensis*, it possesses yellow petals and rosettes of 6–10 leaves. Subspecies *ovatifolia*, however, differs from subsp. *agourensis* by its unbranched caudex, ovate to elliptic basal rosette leaves, green with

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FIGS. 2–4. Photographs of new taxa in *Dudleya*. 2. *Dudleya cymosa* subsp. *agourensis* K. Nakai. a. Isotype plant (0.4×). b. Inflorescence in detail (1.25×). 3. *Dudleya cymosa* subsp. *crebrifolia* Nakai & Verity. a. Holotype plant (0.2×). b. Inflorescence in detail (2×). 4. *Dudleya abramsii* subsp. *affinis* K. Nakai. a. Inflorescence in detail (1.25×). b. Isotype plant (0.5×).



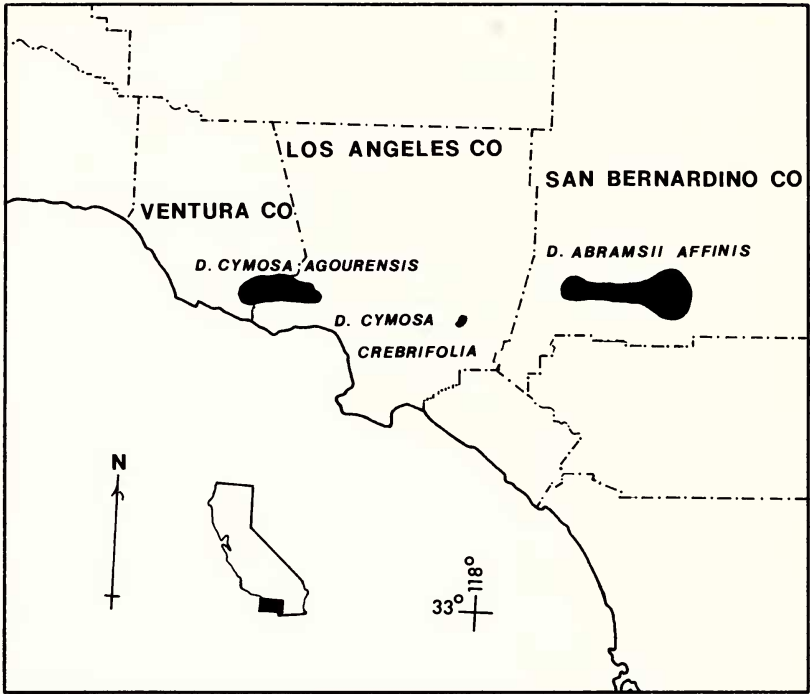


FIG. 5. Geographic distribution of *Dudleya cymosa* subsp. *agourensis*, *D. cymosa* subsp. *crebrifolia*, and *D. abramsii* subsp. *affinis*.

a maroon suffusion on the underside, slightly longer pedicels, and petal apices spreading 90° or more. Subspecies *ovatifolia* is found on the southern slopes of the Santa Monica Mountains on shaded sedimentary rock slopes. In contrast, subsp. *agourensis* is found on the northern slopes of the range on drier, exposed west- to northwest-facing rock outcrops.

Dudleya verityi K. Nakai, also found in the Santa Monica Mountains, has flowers similar to subsp. *agourensis*. This species differs from subsp. *agourensis* by its paler flowers, several to many dichotomously branched stems that may elongate to more than 10 cm long rather than the one or infrequently several cespitosely branched stems that are mostly less than 5 cm long.

***Dudleya cymosa* subsp. *crebrifolia* Nakai & Verity, subsp. nov.**

A subspecies typica caulis simplex, foliis caulis floriferi multibus et crebribus et tardiflorentem differt. Figs. 3a,b, 5.

Caudex 1–2 cm diam. with simple to rarely few branched basal rosettes, 5–12 cm diam., with 6–15 spreading to ascending leaves.

Basal rosettes leaves mostly elliptic to spatulate, acute to acuminate, 4–10(–15) cm long, 2–5 cm wide near the middle, olive-green, rarely glaucous, slightly maroon on the undersurface. Floral stem 10–30(–n50) cm tall, yellowish-green, with 20–50 close-set, horizontal, alternate to subopposite leaves. Inflorescence obpyramidal, with 2–4 branches that branch 1–2 times; cincinnus 2–10 cm long, with 2–15 flowers, pedicels 3–8 mm long. Petals mustard yellow, midribs glaucous, elliptic, acute, 9–10 mm long, 3–3.5 mm wide at the middle, connate 1–1.5 mm, apices spreading to 45°. Chromosome number: $n = 17$. Flowering late June to July (August).

TYPE: USA, CA, Los Angeles Co., San Gabriel Mtns., Fish Canyon, 34°11'N, 117°55½'W, ca. 1.5 km nw. from the mouth of the canyon on n.-facing granitic slopes, common, 400 m. Associated with: *Alnus rhombifolia*, *Umbellularia californica*, *Toxicodendron diversilobum*, *Dudleya lanceolata*, and *D. densiflora*. 25 Jun 1981, K. Nakai 775 (Holotype: CAS; isotype: LA, MO, RSA, SD, US).

PARATYPES: Los Angeles Co., Fish Canyon, *Davidson 3578* (US), *Hood 43-77k* (LA), *Nakai 361* (CAS, LA), *776* (CAS, LA).

Distribution. San Gabriel Mtns., Fish Canyon, 0.5–4 km from the mouth of canyon.

Subspecies *crebrifolia* is distinguished by its mostly solitary basal rosette with mostly elliptic to spatulate leaves, the large number of cauline leaves that are often crowded, and a later flowering period. At the higher elevations (2000 m or more), subsp. *crebrifolia* may still be in flower as late as late July, but when cultivated, it flowers from April to early June. In a letter at US to J. N. Rose (25 Jun 1923), A. Davidson suggested that this plant may be new and noted that one plant had 13 floral stems and the basal rosette leaves were 6 inches (15 cm) long. Subspecies *crebrifolia* is known only in Fish Canyon on vertical granite slopes on both walls of the canyon in partly shaded areas.

Subspecies *crebrifolia* apparently is related most closely to *D. cymosa* subsp. *pumila* and is well within the range of subsp. *pumila*. Although its basal rosettes are often larger than those of subsp. *pumila* from the San Gabriel Mountains, the size is within the overall limit of subsp. *pumila* when plants from the entire geographic range of the latter are compared. Subspecies *crebrifolia* differs from subsp. *pumila* by its elliptic leaves, longer floral stem with 2–3 times the number of cauline leaves that are often crowded together, and a flowering period that is usually 4–6 weeks later. Subspecies *crebrifolia* occurs from 350–600 m, whereas subsp. *pumila*, in the San Gabriel Mountains, occurs below 750 m only in the northern portion of the range [Elizabeth Lake Cyn., elev. 675 m, *Nakai 1015* (LA); elev. 610 m, *Nakai 1016* (LA)].

In Fish Canyon, *D. lanceolata* is common and occasionally grows sympatrically with subsp. *crebrifolia*. *Dudleya lanceolata* is similar

to subsp. *crebrifolia* in basal rosette size, length of the floral stem, and petal color. Infrequently, the number of cauline leaves in *D. lanceolata* is similar to those of subsp. *crebrifolia*. *Dudleya lanceolata* differs from subsp. *crebrifolia* in its lanceolate, often glaucous, leaves, a more lax inflorescence, and an earlier flowering period. *Dudleya lanceolata* is tetraploid ($n = 34$), whereas subsp. *crebrifolia* is a diploid.

DUDLEYA ABRAMSII Rose subsp. **ABRAMSII**—*Dudleya abramsii* Rose in Britton & Rose, Bull. N.Y. Bot. Gard. 3:14. 1903.—*Cotyledon abramsii* Fedde, Bot. Jahresber. Just. 31:826. 1904.—*Echeveria abramsii* Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:477. 1930.—**TYPE:** USA, CA, San Diego Co., wet crevices of rocks west of Jacumba, 1 Jun 1903, *Leroy Abrams 3707* (Holotype: US!, photo LA!; isotype: DS!, GH!, NY!, POM!, UC!, US!).

Caudex diameter 1–3 cm thick, mostly less than 5 cm long, unbranched or 5–20(–75) cespitose branches. Basal rosette 2–8(–15) cm diam. consisting of 8–25 erect or ascending oblong-lanceolate, acute to acuminate, glaucous leaves, apiculate, 1–10 cm long, 3–15 mm wide, 1–4 mm diam., plane or concave ventrally, rounded dorsally, the base 5–15 mm wide. Floral stem 2–25 cm tall, 1–5 mm diam. Cauline leaves 3–20, ascending, triangular-lanceolate, acute, the lowermost 0.5–3 cm long, 2–11 mm wide. Inflorescence of 2–3 simple to once or twice bifurcate ascending branches or obpyramidal. Cincinnus 3–15 cm long, with 2–10(–20) flowers. Pedicels erect, 0.5–5(–11) mm long. Calyx 3–5 mm wide, 3–6 mm high, subtruncate to tapered below, the segments triangular-ovate to lanceolate, acute, 2–5 mm long, 1.5–3 mm wide. Petals pale yellow, often with red vertical lines particularly along the midrib, elliptic to narrow lanceolate, acute, occasionally erose, erect with petal apices often spreading to 90°, 8–13 mm long, 2–3 mm wide, connate 1–4.5 mm. Epipetalous filaments 2.5–6 mm long, adnate 1–3 mm; antesepalous filaments 4.5–8 mm long, adnate 2–4 mm; anthers yellow, 1–1.5 mm long. Gynoecium erect, slender, attenuate, 4–7 mm high, ovary 3–5.5 mm long, styles 0.5–2 mm long. Nectaries reniform, pale yellow, 0.5–1 mm long. Chromosome number: $n = 17$. Flowering April to June.

Distribution. USA, CA, Riverside Co., San Jacinto Mtns., San Diego Co., Laguna Mtns.; MEXICO, Baja California Norte, Sierra Juarez and Sierra San Perdo Martir. Elev. 750–1750 m.

The label data from the type specimens varies, and thus, the exact type locality is uncertain. The holotype and an isotype specimen at NY, both of which are a plant cultivated by Rose, are labeled “five miles [6.7 km] west of Jacumba”. The specimen at POM, however,

is labeled "Walker's Ranch, near Jacumba". Others, including an isotype at US, are labeled "two miles [2.7 km] west of Jacumba". Because Abrams spent most of his academic career at Stanford University, one would suspect that the specimen at DS would have an accurate label. I was able to collect *D. abramsii* 2 mi west of Jacumba, but I was unable to find it 5 mi west of Jacumba.

Moran (1951) listed two populations of *D. abramsii* from the San Jacinto Mountains, one from near Kenworthy [Munz 5788 (POM)] and the other from Taquitz (sic) Ridge, 9000 ft (2770 m) [Jaeger in 1921 (POM)]. The population near Kenworthy is *D. abramsii*, but differs from typical *D. abramsii* by lacking the characteristic red striations along the petal midrib. The specimen from Tahquitz Ridge differs considerably from the Kenworthy population in its comparatively broad, oblong to ovate leaves and short floral stem. It resembles no specimens of *D. abramsii* that I have studied. The "Tahquitz" specimen, however, does resemble plants of *D. cymosa* subsp. *pumila*. A recent collection made near Tahquitz Ridge by J. Catlin [Lily Rock, near Idlywild, 2300 m, Nakai 984 (CAS, LA)] has reddish flowers and is similar to the "Tahquitz" specimen. Catlin (pers. comm.) reports similar plants on Suicide Rock, across Strawberry Valley from Lily Rock, and along Snow Creek on the north slope of San Jacinto Peak. The status of these populations is uncertain until more material can be studied, but it appears they are not *D. abramsii*.

Dudleya abramsii* subsp. *callicola (Bartel & Shevock) K. Nakai, comb. nov. — *Dudleya callicola* Bartel & Shevock, Madroño 30: 210. 1983. — TYPE: USA, CA, Tulare Co., Kern River at Roads End, T23S R32E S13, Sequoia National Forest, 1200 m, 11 Jul 1981, Shevock 8802 (Holotype: CAS!, photo LA!; isotype: FSC, NY!, RSA!, SBBG, SD!, UC).

Distribution. USA, CA, southern Sierra Nevada from the Rincon area south of Durrwood Creek in Tulare Co. to the southern Piute Mtns. in Kern Co. Elev. 500–1550 m.

Collections I have made from the Piute Mountains, the vicinity of Lake Isabella, and along the Kern River suggest that *D. callicola* is closer to *D. abramsii* than previously believed. Bartel and Shevock (1983) suggested that *D. callicola* was intermediate between *D. abramsii* and *D. cymosa*, but closer to *D. abramsii*. They noted that *D. callicola* was distinct from *D. abramsii* in its 1) heavier foliar bloom, 2) obpyramidal inflorescence with a thicker floral stem and spreading cincinni versus a comparatively simple inflorescence and ascending cincinni, 3) slightly longer pedicel, 4) pale yellow petals unmarked with red, and 5) occurrence predominately on limestone.

The type locality of *D. callicola* is the limestone outcrops above

Roads End along the Kern River in Tulare Co., but I have observed plants resembling *D. calcicola* at a number of localities along the Kern River on substrates other than limestone. For example, one population was found less than 0.5 km north of the type locality on metamorphic rock. Pedicel length from cultivated plants from 12 populations of *D. abramsii* and 13 populations of *D. calcicola* exhibited no differences. They measured 3–7 mm ($\bar{X} = 5$ mm) for *D. abramsii* and 3–8 mm, ($\bar{X} = 5$ mm), for *D. calcicola*. Measurements made from herbarium specimens, however, ranged from 2–10 mm ($\bar{X} = 5$ mm), for *D. abramsii* and from 2–12 mm ($\bar{X} = 6$ mm) for *D. calcicola*. Although several populations of *D. calcicola* do have flowers with plain, pale yellow petals, others have the characteristic *D. abramsii* red striations along the petal midrib. Cultivated plants I collected from the type locality and observed for five flowering seasons had flowers with petals conspicuously marked with red. In at least three populations of *D. abramsii* [MEXICO, Baja California Norte, Cerra Blanco, *Moran 17608* (SD); 2 km w. of Rancho Santa Cruz, Sierra San Pedro Martir, *Moran 23461* (SD), *Nakai and Prigge 1136* (CAS, LA); USA, CA, Riverside Co., Kenworthy, *Munz 5788* (POM, SD), *Nakai 1007* (CAS, LA)] the petals lack red pigment. The density of the foliar bloom does not appear to differ between the two taxa.

Typical *D. calcicola* is a densely-packed plant with up to 50 rosettes. Bartel and Shevock (1983), however, cite populations (e.g., Long Canyon) that have plants with one to a few rosettes. In the Laguna Mountains of San Diego Co., the higher elevation populations of *D. abramsii* also have plants with 50 or more rosettes, and a population of a *D. abramsii* subsp. *affinis* K. Nakai in Cushenbury Canyon has densely-packed plants with up to 50 rosettes. Thus, the number of rosettes per plant may not differ between the taxa.

An important character in which *D. calcicola* is similar to *D. abramsii* is the relative lengths of the antesealous and epipetalous stamens. In *D. cymosa*, the difference in staminal length is often small (<0.5 mm). In both *D. abramsii* and *D. calcicola*, the difference is usually 1–1.5 mm. This strongly supports a close relationship between *D. calcicola* and *D. abramsii*.

Another character that distinguishes *D. calcicola* from *D. abramsii* is the inflorescence. Although the inflorescence of *D. calcicola* found in the wild may be similar to *D. abramsii*, cultivated plants consistently have an obpyramidal inflorescence consisting of 2–4 branches that bifurcate once or twice. Cultivated plants of *D. abramsii* have a simpler inflorescence of 2–3 mostly simple branches. Cultivated *D. calcicola* tends to have more cauline leaves (8–15) in comparison to *D. abramsii* (2–8).

Although there are enough differences to warrant taxonomic recognition, the two taxa have considerable overlap in most of the key

characters. Of additional interest are two collections from the geographic range of *D. calcicola* that were identified by authorities as *D. abramsii*: one from the Tehachapi Mtns. [May 1925, Davidson 3599 (US)], annotated by Rose; another collected by J. Zavinowich from Jawbone Canyon on the east slope of the Piute Mtns. [Moran 24196 (SD)], determined by Moran. These two authorities on *Dudleya* apparently also recognized the resemblance of this material to *D. abramsii*. Thus, I proposed the combination *D. abramsii* subsp. *calcicola*.

***Dudleya abramsii* subsp. *affinis* K. Nakai, subsp. nov.**

A subspecies *typica* caudice simplicis, foliis rosulae oblanceolatis vel ellipticis differt. Figs. 4a,b, 5.

Plants simple, rarely cespitously branched. Basal rosette 3–6 cm diam., of 10–25 oblanceolate to elliptic, glaucous leaves, 2–4 cm long, 7–15 mm wide; apices acute to acuminate. Cauline leaves lanceolate, glaucous, 5–6 mm long, 2–3 mm wide, acute. Floral stem erect, 5–11 cm long, pale yellow to glaucous. Inflorescence of 2–3 mostly simple branches, cincinnus ascending, 2–8 cm long, with 3–8 flowers, lowermost pedicels 2.5–8 mm long. Petals pale yellow with red striations along the midribs, connate 1.5–2.5 mm, apices spreading to 90°. Epipetalous filaments 2.5–4 mm long, antesealous filaments 3.5–6 mm long. Chromosome number: $n = 17$. Flowering May to July.

TYPE: USA, CA, San Bernardino Co., San Bernardino Mtns., Green Canyon, ca. 0.5 km sw. of National Forest Road 2N93 on trail to Sugarloaf Mountain where the trail crosses the creek, 34°13'N, 116°48'W, on e. side of creek on granite; common; 2600 m; with *Juniperus*, *Pinus*, *Cercocarpus*, *Echinocerus*. 28 Jun 1984, K. Nakai 1146 (Holotype: CAS; isotype: LA, NY).

PARATYPES: USA, CA, San Bernardino Co., confluence of Deep and Hook creeks, Nakai 1110 (CAS, LA), 1114 (CAS, LA, RSA); Holcomb Creek, 8 km sw. of Big Pine Flat, Nakai 1153 (LA); nw. slope of Gold Mountain, 3.2 km w. of Big Bear refuse dump, Nakai 1151 (CAS, LA); n. shore of Lake Baldwin, D. B. Stark 4992 (RSA), Nakai 702 (CAS, LA); Johnson Grade, Peirson 8972 (POM, UC), Peirce s.n. (POM), Moran 2193 (UC), Nakai 1145 (CAS, LA); ridge e. of Lake Baldwin, Munz 10494 (POM); plateau s. of Lake Baldwin, Peirson s.n. (RSA); Cushenbury Canyon, Deburg 2608 (RSA), Nakai 1147 (CAS, LA); Cushenbury Spring, Parish 1629 (POM); Green Canyon, Clausen & Trapido 4770 (CU, NY, US, WTU), Nakai 1113 (CAS, LA).

Distribution. North slopes of the San Bernardino Mtns. from 1800–2600 m on granite, quartzite, or, rarely, limestone.

Dudleya abramsii subsp. *affinis* differs from subsp. *abramsii* by

its mostly unbranched caudex and basal rosette leaves that are oblanceolate to elliptic rather than oblong-lanceolate. Some plants of subsp. *affinis* resemble *D. cymosa* subsp. *pumila*, particularly in rosette size, leaf shape, and, in more robust plants, the inflorescence. The most consistent differences are a shorter pedicel length, pale yellow petals with red striations, and the difference in length between the antesepalous and epipetalous stamens.

Plants from Cushenbury Canyon grow on limestone and differ from typical plants of subsp. *affinis* by their several to many branched caudex and smaller rosettes, 1.5–3 cm in diameter. This population seems similar to subsp. *calcicola* and subsp. *abramsii*. It differs from subsp. *calcicola* by its more simple inflorescence and from subsp. *abramsii* by its rosette leaf shape. Although this population is intermediate between these three subspecies of *D. abramsii*, I presently consider this population an aberrant form of subsp. *affinis*.

KEY TO SPECIES AND SUBSPECIES

- A. Pedicels 5–20 mm long; petals connate 1–2.5 mm; the difference between epipetalous and antesepalous staminal length is usually <0.5 mm.
 - B. Basal rosette leaves evergreen, 2–17 cm long, 0.5–6 cm wide; caudex more than 1 cm diam.
 - C. Floral stem mostly 1.5–4.5 dm tall.
 - D. Floral stem with 20–50 close-set leaves; basal rosette leaves elliptic to spatulate. San Gabriel Mtns., s. California *D. cymosa* subsp. *crebrifolia*
 - D. Floral stem usually with <20 leaves; basal rosette leaves oblong-oblanceolate to oblong-triangular, rarely spatulate. Central and n. California.
 - E. Petals bright yellow to red; rosette leaves oblong-oblanceolate, rarely spatulate, 1–6 cm wide. Coast Range from the Salinas River, Santa Clara Co., n. to Humboldt Co.; Sierra Nevada
. *D. cymosa* subsp. *cymosa*
 - E. Petals pale yellow.
 - F. Basal rosette leaves oblong to oblanceolate; inflorescence of 2–3 bifurcate branches; pedicels 6–12 mm long. Inner South Coast Range from Contra Costa Co., to w. Fresno and ne. Monterey cos., on various rock substrates
. *D. cymosa* subsp. *paniculata*
 - F. Basal rosette leaves oblong-triangular; inflorescence of 2–3 simple branches; pedicels 4–7 mm long. Santa Clara Valley on serpentine
. *D. cymosa* subsp. *setchellii*

- C. Floral stem mostly < 1.5 dm tall. Outer South Coast Range from the Salinas River s. to s. California.
- G. Basal rosette leaves oblanceolate to spatulate, usually 10–25, mostly short acuminate to cuspidate. Outer South Coast Range to San Gabriel and San Bernardino mtns. *D. cymosa* subsp. *pumila*
- G. Basal rosette leaves oblong to elliptic or ovate, usually 6–10, acute to acuminate.
- H. Basal rosette leaves ovate, green, often with a maroon suffusion on the underside; caudex unbranched. Santa Monica and Santa Ana mtns. *D. cymosa* subsp. *ovatifolia*
- H. Basal rosette leaves oblong to elliptic, glaucous; caudex simple or few to, rarely, several branches. Santa Monica Mtns. *D. cymosa* subsp. *agourensis*
- B. Basal rosette leaves withering in summer, 1.5–4 cm long, 5–12 mm wide; caudex < 1 cm diam. *D. cymosa* subsp. *marcescens*
- A. Pedicels 0.5–7 mm long; petals connate 1.5–4.5 mm; the difference between the epipetalous and antesepalous staminal length is usually 1–1.5 mm.
- I. Basal rosette leaves oblong to oblong-lanceolate; plants with few to many branches.
- J. Inflorescence of 2–3 mostly simple branches; pedicels mostly < 5 mm long; petals usually with red striations along the midribs.
- K. Lower cauline leaves usually < 15 mm long; floral stem 2–15 cm tall; petals connate 2–4.5 mm. San Jacinto Mtns., Riverside Co., and Laguna Mtns., San Diego Co.; Sierra Juarez and Sierra San Pedro Martir, Baja California Norte *D. abramsii* subsp. *abramsii*
- K. Lower cauline leaves 10–30 mm long; floral stem 5–25 cm tall; petals connate 1.5–3 mm. San Luis Obispo Co. *D. abramsii* subsp. *murina*
- J. Inflorescence of 2–3 simple to usually bifurcate branches; pedicels 3–8 mm long; petals with or without red striations along the midribs. Southern Sierra Nevada *D. abramsii* subsp. *calcicola*
- I. Basal rosette leaves elliptic to oblanceolate; plants usually unbranched. San Bernardino Mtns., San Bernardino Co. *D. abramsii* subsp. *affinis*

Additional specimens of *Dudleya* that were cultivated and examined but not cited in the text. Collection numbers, unless otherwise noted, are the author's.

DUDLEYA ABRAMSII: subsp. ABRAMSII—USA, CA, Riverside Co.: San Jacinto Mtns.,

near Kenworthy, 1059. San Diego Co.: Mt. Laguna, 454; Laguna Mtns., Kwaaymit Pt., 1180; Descanso Junction, 845; Kitchen Creek, 844; Corte Madera Lake, *Van Der Werff s.n.*; Campo 840; Jacumba, 841; Dubber Spur, 842. MEX, Baja Calif. Norte: Sierra Juarez, near Laguna Hansen, *Prigge 5098*; n. of Valle Trinidad, *Verity s.n.*; Sierra San Pedro Martir, between Mike Sky Ranch and El Burro, *Verity and Prigge s.n.*; w. of Rancho Santa Cruz, *Nakai and Prigge 1136*. Subsp. CALCICOLA—USA, CA, Tulare Co.: ½ km n. of Road's End, 1080; Road's End, 825; Hospital Flat Campground, ca. 9.5 km n. of Kernville, 1078. Kern Co.: 2.0 km s. of Kernville, 1077; 8 km s. of Kernville, 827; Long Canyon, 828; near Mountain Mesa, 829; Bodfish Cyn., 830; s. of Bodfish, 831; near Twin Oaks, 678; near Loraine, 679, 680; Caliente, 832; Cottonwood Creek, near Kelso Valley, 676, 677.

DUDLEYA CYMOSA: subsp. CYMOSA—USA, CA, Mendocino Co.: Hopland, *McCabe 356*. Sonoma Co.: near Mt. St. Helena, *Almeda s.n.*; Cazadero, 973. Marin Co.: Bolinas Bay, 975; Stinson Beach 398; s. of Stinson Beach, 398; Mt. Talmapais, 399. Solano Co.: s. of American Cyn. Rd., 821; Mix Cyn., Vaca Mtns., 531. Santa Cruz Co.: Eagle Rock, *McCabe 369*. Santa Clara Co.: Lexington Reservoir, 814; New Almaden, 814; Loma Prieta, 813; Stevens Creek, 1088. Tehama Co.: near Paynes Creek, 961. Sierra Co.: w. of Downieville, *McCabe 507*. Nevada Co.: near Nevada City, 951. Placer Co.: Applegate, 950. Amador Co.: near Ione, 532; w. of Volcano, 394; Volcano, 534; near Mokelumne River, 535. Calaveras Co.: near San Andreas, 536; near Kentucky House, 393, 537. Tuolumne Co.: Table Mtn., 1087; near Coulterville, 538. Mariposa Co.: near Yosemite Valley, 1084, 1085; near Bear Valley, 539, 822. Inyo Co.: Sawmill Creek, 1081. Tulare Co.: near Springville, 392; w. of Pierpoint, 823. Kern Co.: Bear Hollow Creek, 1075; Shirley Creek, 1076. Subsp. PANICULATA—Contra Costa Co.: n. slope of Mt. Diablo, 949; Mt. Diablo, 396; s. slope Mt. Diablo, 948. Alameda Co.: Palomare Rd., 820; Welch Creek, 819. Santa Clara Co.: Coyote Reservoir, 818; Alum Rock, 817; Mt. Hamilton, 816; Anderson Reservoir, 977; Coyote Lake, 978. Stanislaus Co.: Arroyo del Puerto, 946, 947. Merced Co.: Pacheco Pass, 945. San Benito Co.: Pinnacles, 809; near Panoche Pass, 944; Clear Creek, 942. Monterey Co.: Lewis Creek, 808; Lorenzo Creek, 628, 1085; Bull Cyn., 1092. Fresno Co.: Coalinga Hot Spr., *McCabe 501*. Subsp. PUMILA—Monterey Co.: Pine Valley, 526; n. of Castro Cyn., 631; s. of Castro Cyn., 632; n. of Mission San Antonio, 523, 524; Nacimiento-Fergusson Rd., 100 m, 410; Nacimiento-Fergusson Rd., 700 m, 409, 633. Santa Barbara Co.: Santa Barbara Cyn., 788; Rattlesnake Cyn., 1100. Ventura Co.: confluence of Potrero John and Sespe creeks, 544; Sespe Gorge, 545, 789. Los Angeles Co.: Elizabeth Lake Cyn., 825 m, 1013; 790 m, 1014; 670 m, 1015; 610 m, 1016; Arroyo Seco, 915 m, 430; 850 m, 553; 1070 m, 555; Hidden Springs, 383, 427; San Gabriel Cyn., 1500 m, 1125; 1600 m, 1126; 1700 m, 1021. San Bernardino Co.: San Antonio Falls, 1900 m, 689; Waterman Cyn., 386, 1183; s. of Crestline 1184; Miller Cyn., 1185; Little Mill Creek, 700; Keller Mtn., 702, 1143; Skinner Creek, 1148.

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